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Greening of the land surface in the world's cold regions consistent with recent warming

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Abstract

Global ecosystem function is highly dependent on climate and atmospheric composition, yet ecosystem responses to environmental changes remain uncertain. Cold, high-latitude ecosystems in particular have experienced rapid warming¹, with poorly understood consequences^{2,3,4}. Here, we use a satellite-observed proxy for vegetation cover—the fraction of absorbed photosynthetically active radiation⁵—to identify a decline in the temperature limitation of vegetation in global ecosystems between 1982 and 2012. We quantify the spatial functional response of maximum annual vegetation cover to temperature and show that the observed temporal decline in temperature limitation is consistent with expectations based on observed recent warming. An ensemble of Earth system models from the Coupled Model Intercomparison Project Phase 5 (CMIP5) mischaracterized the functional response to temperature, leading to a large overestimation of vegetation cover in cold regions. We identify a 16.4% decline in the area of vegetated land that is limited by temperature over the past three decades, and suggest an expected large decline in temperature limitation under future warming scenarios. This rapid observed and expected decline in temperature limitation highlights the need for an improved understanding of other limitations to vegetation growth in cold regions^{3,4,6}, such as soil characteristics, species migration, recruitment, establishment, competition and community dynamics.

Main

A global increase in green vegetation has been observed over recent decades^{7,8} and widely attributed to both direct and indirect anthropogenic influences—primarily elevated atmospheric CO₂, but also changes in climate, nitrogen deposition and land use change^{8,9,10,11}. The global greening has contributed to changes in biophysical feedbacks such as evapotranspiration and albedo¹², along with an increased terrestrial carbon sink¹³, which together have served to slow the rate of global warming². However, uncertainties remain regarding the drivers of the reported greening and their spatial variation, and thus the likelihood of continued greening.

Ecosystems in cold regions in particular have exhibited rapid increases in green vegetation^{3,7}. Plot-scale evidence suggests a link to warming^{4,6}, but direct attribution of observed regional trends to environmental changes

has been elusive. Regional studies have relied on multi-factorial simulation experiments with global vegetation models^{8,11,14}, but vegetation models are known to perform poorly for high-latitude and cold-limited ecosystems^{15,16,17}, overestimating both the extent of green vegetation and the trend in recent decades¹⁷. Model results suggest a role of climate change and CO₂ in the observed greening trend^{8,10,11,14,18}, but direct attribution is hindered by model spread and uncertainty¹⁴.

Here, we develop a data-based approach^{19,20}, using three decades of remotely sensed estimates of the fraction of absorbed photosynthetically active radiation (fAPAR)—a proxy for productive foliage cover²¹—to characterize the relationship between maximum annual foliage cover (F_{\max}) and the summer warmth index (SWI₅; the sum of the monthly mean temperatures above 5 °C). We use the approach, which was originally developed for water-limited ecosystems^{19,20}, to identify the spatial distribution of ecosystems in which F_{\max} is limited by temperature, and thus to track changes in temperature limitation over time. By estimating the temperature (T) sensitivity of F_{\max} (γ_F^T) using spatial gradients, and comparing this with expected changes in F_{\max} due to observed changes in temperatures, we show a long-term increase in foliage cover that is consistent with the expected influence of recent warming. The observed greening occurred together with a large decline in the spatial extent of temperature limitation over recent decades, in particular for northern high-latitude ecosystems. Finally, we use an ensemble of global Earth system models (ESMs) from the recent Coupled Model Intercomparison Project Phase 5 (CMIP5) to examine the impact of future projected temperature changes on the spatial extent of temperature limitation, and to assess the ability of ESMs to estimate the sensitivity of maximum foliage cover to changes in temperature.

Our functional responses analysis of global satellite observations from the Global Inventory Modeling and Mapping Studies third-generation fAPAR data product (GIMMS3g⁵) shows the spatial dependence of vegetation cover on temperature (Fig. 1), with low maximum foliage cover in colder regions (low SWI₅) and high maximum foliage cover in warmer regions. We examined the ninety-fifth percentile of the distribution of annual F_{\max} (F_{95} (%)), which characterizes the maximum F_{\max} attained globally for a given annual SWI₅. We delineated the regions where temperature strongly affected F_{\max} and found that it depended linearly on SWI₅ under colder conditions (Fig. 1). The slope of the F_{95} edge quantifies γ_F^T (the percentage change in F_{95} per degree change in SWI₅; % °SWI⁻¹), and the temperature at saturation (mean \pm s.d. SWI₅ = 43.2 \pm 1.36 °C) delineates the region where F_{\max} is limited by temperature (Fig. 1 and Supplementary Fig. 1).

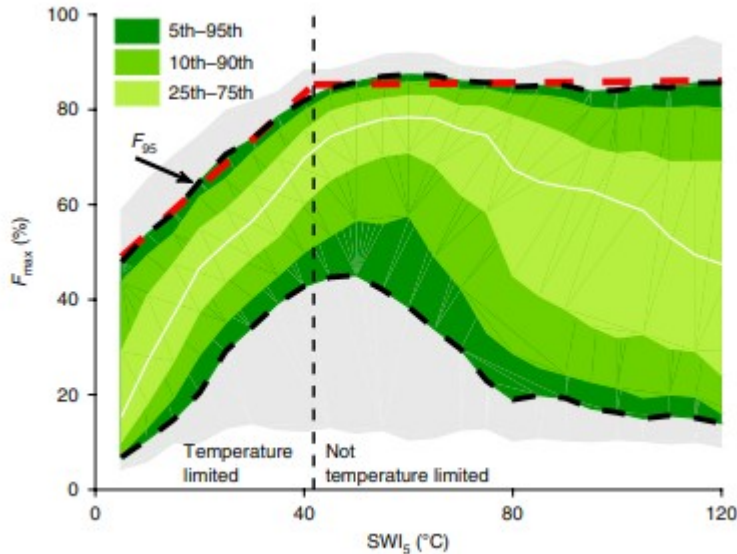


Figure 1. Spatial relationship between SWI_5 and F_{max} for the three-year period from 1982–1984. F_{95} in each 5 °C bin represents the maximum attainable F_{max} for a given annual SWI_5 (black dashed line; indicated by arrow). A breakpoint regression applied to the ninety-fifth percentile approximates the sensitivity of F_{max} to spatial changes in SWI_5 (red dashed line), and delineates regions where F_{max} is temperature limited and those where it is not, as either below or above the breakpoint (vertical dashed line).

We examined changes in the slope and intercept of F_{95} during the GIMMS3g observational record (1982–2012) and found both an increasing intercept (mean \pm 95% confidence interval: $4.16 \pm 1.47\%$ decade⁻¹) and a declining slope ($-0.10 \pm 0.05\%$ decade⁻¹) (Fig. 2) for F_{95} relative to the baseline SWI_5 from 1982–1984. An increasing intercept indicates an increase in F_{95} in regions that were temperature limited at the start of the measurement record, with a $26.5 \pm 1.9\%$ increase in F_{95} in the most temperature-limited regions (Fig. 2 and Supplementary Fig. 2). A decreasing slope implies that regions that were more temperature limited at the start of the observational record are greening faster than regions that were less temperature limited. The changes in the relationship between F_{max} and SWI_5 in temperature-limited regions are consistent with accelerated warming in colder regions¹ and could indicate a change in temperature limitation over time.

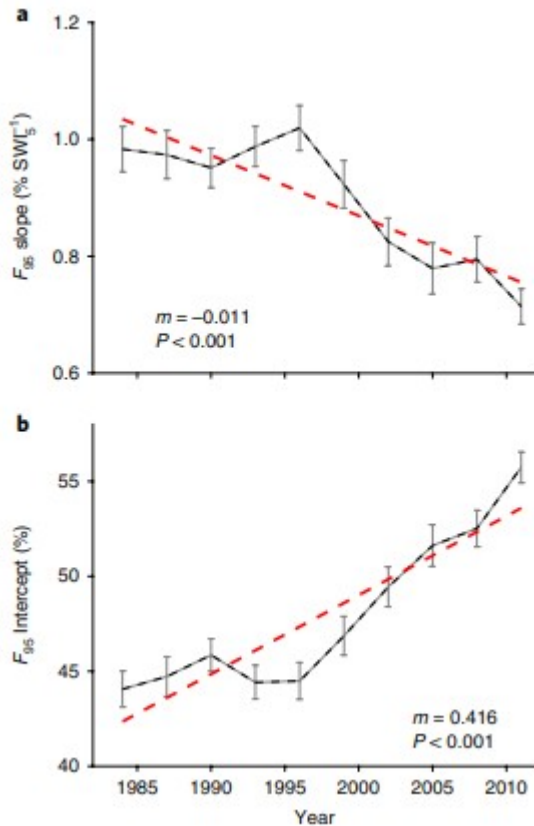


Figure 2. a,b, Slope (a) and intercept (b) of the relationship between F_{95} and SWI_5 . Error bars represent 95% confidence intervals. The red dashed lines show fitted linear regressions, with slope m (a, $\% SWI_5^{-1} yr^{-1}$; b, $\% yr^{-1}$) and P values indicated.

We used a space for time substitution to examine whether the observed changes in F_{max} in temperature-limited regions are consistent with observed long-term (1982–2012) changes in temperature. To do so, we predicted the expected change in F_{95} ($F_{95} = I + \Delta T \Delta F_{95}$), where I and ΔF_{95} are estimated as the intercept and slope of the relationship between F_{95} and SWI_5 from the start of the observational record (1982–1984), and SWI_5 is temporally dynamic throughout the observational record. The change in F_{95} over time, predicted based on temporally static spatial changes in F_{95} , was statistically equivalent to the observed long-term change ($P < 0.01$, Chow test; Fig. 3). Observed temperature changes implied a somewhat lower increase in F_{95} in the most temperature-limited regions ($19.12 \pm 2.27\%$; Fig. 3), but with a smaller decline in the F_{95} slope over time than observed. The concordance of the observed and expected change in F_{95} suggests that the observed long-term increase in F_{max} is consistent with a response to long-term warming, although other factors such as CO_2 fertilization and nitrogen deposition could also play a role.

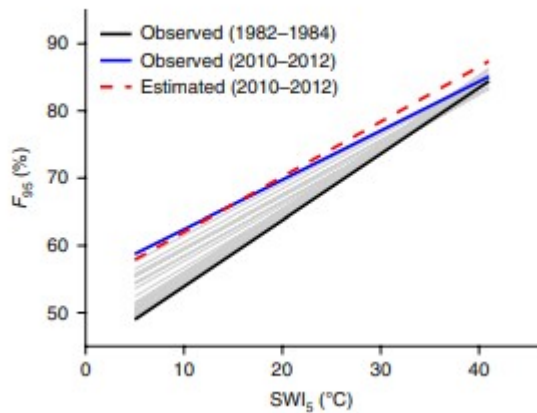


Fig. 3: Observed and predicted changes in F_{95} . Each solid line represents the observed F_{95} for a specific three-year period, starting from 1982–1984 (black) and ending in 2010–2012 (blue). Grey lines show F_{95} for intermediate three-year periods. The red dashed line represents the predicted temporal change in F_{95} based on the observed spatial sensitivity to SWI_5 and observed long-term changes in SWI_5 .

Ecosystems below the temperature-limitation threshold in the relationship between F_{95} and SWI_5 (Fig. 1) represented $19.87 \pm 0.67\%$ of the total vegetated area of the extratropical northern latitudes at the start of the measurement record (1982–1984), and are primarily located at high latitudes and on the Tibetan Plateau (Fig. 4). Our results indicate that the spatial extent of temperature limitation of F_{max} has declined by $16.35 \pm 0.64\%$ over the observational record. The release from temperature limitations was largely experienced at the southern edge of high-latitude ecosystems. We estimate 45 and 85% reductions in the temperature-limited area by 2100 for CMIP5 ensemble warming projections under Representative Concentration Pathways (RCPs) 4.5 and 8.5, respectively (Fig. 4).

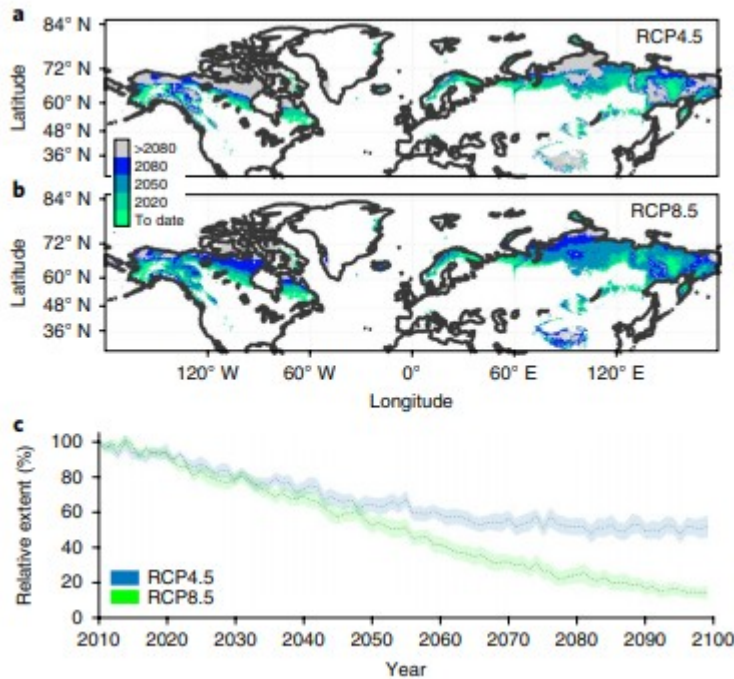


Fig. 4: Current and predicted changes in the relative spatial extent of temperature-limited area of vegetated land. a,b, Shaded areas represent areas where F_{\max} indicated temperature limitation at the start of the observational record (1982–1986), but did not by the corresponding year. Green areas represent the change in the observational record to 2010, whereas other shades represent projected changes based on temperature projections from the CMIP5 models under RCP4.5 (a) and RCP8.5 (b). c, Proportion of vegetated areas that are temperature limited over time, relative to the extent of vegetated areas that were temperature limited at the end of the measurement record (2010–2012). The means (dashed lines) and standard errors (shaded areas) of ten ESMs (Supplementary Table 1) from the CMIP5 ensemble under RCP4.5 (blue) and RCP8.5 (green) are shown.

By focusing on the ninety-fifth percentile, the space for time substitution utilized here minimizes the influence of other limitations to growth^{19,20}, thus allowing for identification of the independent temperature sensitivity. However, in reality, multiple factors limit maximum vegetation cover in cold regions, including nutrient availability, rooting depth, permafrost dynamics and soil moisture. We estimate that 44% of the vegetated land surface identified as temperature limited is primarily temperature limited, defined as being within $\pm 10\%$ of the potential F_{\max} (Supplementary Figs. 3 and 4). This proportion suggests that the vegetation cover response to warming of the remaining 56% will probably be mediated by other factors. Indeed, the mean (\pm s.e.) long-term increase in maximum vegetation cover for vegetated areas that are primarily temperature limited was $1.48 \pm 0.05\% \text{ decade}^{-1}$, whereas vegetated areas limited by both temperature and other factors had smaller increases of $0.8 \pm 0.03\% \text{ decade}^{-1}$. The predicted declines in the temperature-limited area therefore do not necessarily translate into a uniform increase in vegetation cover. For instance, warming also extends the growing season length, which may lead to earlier snow-melt, increase peak season water stress, and thus reduce vegetation

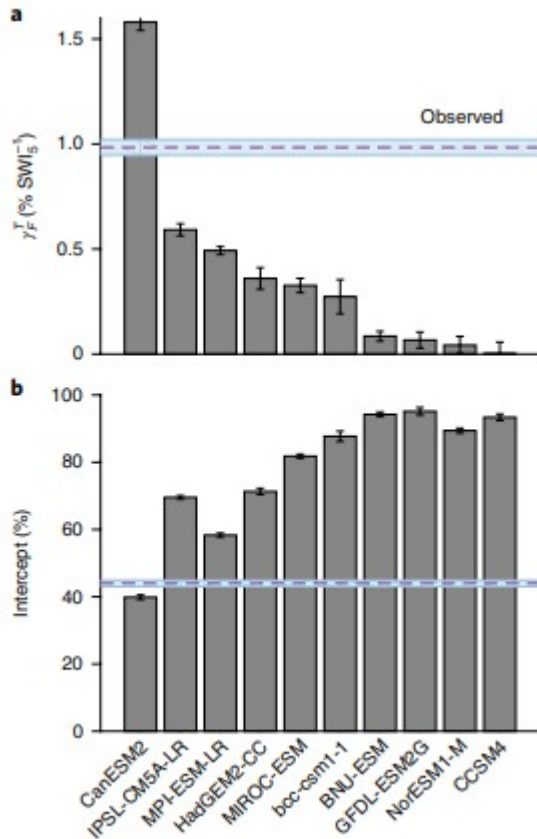


Fig. 5: ESM estimates of the relationship between maximum vegetation cover and temperature. a,b, The modelled γ_{FT} (a) and intercept (b) for each CMIP5 model (grey bars, mean ± 1 s.d.) are estimated using the relationship between F_{95} and SWI_5 based on ESM-modelled temperatures. The observed γ_{FT} (a) and intercept (b) (blue horizontal shading, mean ± 1 s.d.) are estimated from the relationship between GIMMS3g F_{95} and SWI_5 based on Climatic Research Unit monthly temperatures. Model details are provided in Supplementary Table 1 and individual model functional responses are presented in Supplementary Fig. 5.

The greening of the Earth is a widespread phenomenon—one that models have primarily attributed to changes in atmospheric CO_2 and climate^{8,11}. Here, we use direct observations to isolate the functional response of vegetation cover to temperature in temperature-limited regions, and report an observed greening consistent with the effect of long-term temperature changes. The identified temperature sensitivity shows that growing season warmth is a dominant factor for vegetation production in cold regions, confirming previous reports of temperature controls on both spatial and temporal vegetation dynamics^{27,28,29}. Our analysis also suggests a large reduction in ecosystem temperature limitation under future warming, although other limitations will probably play a large role in mediating the extent to which high-latitude ecosystems green. For example, arctic tundra soils are nutrient poor and, through stoichiometric requirements, impose limits on potential biomass, although mineralization of previous frozen soil nitrogen may³⁰ or may not³¹ offset those limitations. Similarly, the waterlogged soils of extensive northern wetlands are unsuitable for dense

vegetation, regardless of the temperature limitation. Other limitations include the limited ability of species to migrate and adapt to the distinct environmental conditions of high-latitude ecosystems^{23,24}. Current models need to accurately reproduce the effect of temperature on vegetation cover. That said, the expected release from temperature limitation under future warming highlights the importance of non-temperature limitations in mediating ecosystem responses to future climate change.

Methods

Satellite data

We used estimates of the fAPAR from GIMMS3g⁵, available for the period 1982–2012. Datasets are provided biweekly at 0.083° spatial resolution and were regridded to match the spatial resolution of the climate data. F_{\max} was calculated as the maximum recorded value during each year. fAPAR is closely related to the photosynthetic activity of plants, and therefore constitutes an indicator of the presence and productivity of live vegetation.

Climatic variables

Monthly fields of air temperature at a 0.5° spatial resolution were obtained from the Climatic Research Unit high-resolution gridded datasets version 3.24 (ref. 32). The monthly mean air temperature values were converted to annual values of summer warmth by summing all monthly temperature values above a baseline of 5 °C (SWI_5). This approach is designed to account for changes in temperatures that effect vegetation growth, while minimizing changes in temperatures that are too low to influence vegetation. Using a base temperature of 0 °C (SWI_0) led to the inclusion of low-temperature and low-fAPAR pixels that were relatively insensitive to temperature change, but did not affect the overall results (Supplementary Fig. 6).

Breakpoint regression analysis

Three-year running-mean F_{\max} values were binned according to their corresponding temperature values for 5° temperature bins^{19,20}. For each bin, the upper and lower ninety-fifth, ninetieth and seventy-fifth percentiles were determined for each running-mean block. Breakpoint regression was applied to the ninety-fifth percentile values (F_{95}) using multi-phase linear regression. We estimated uncertainties of fit parameters through Monte Carlo simulations of zero-mean deviates based on the Cholesky decomposition of the covariance matrix. The regression of the ninety-fifth percentile of F_{\max} represents the maximum F_{\max} attainable for a given SWI_5 , thus minimizing the influence of other factors, such as precipitation or aridity, on the derived responses (Supplementary Fig. 8). The breakpoint of the regression identifies the region where the vegetation–temperature relationship plateaus and vegetation ceases to be temperature limited. Note that the breakpoint temperature was relatively insensitive to the percentile used (Supplementary Fig. 7). We constructed time series of the

slopes and intercepts of the breakpoint regression, and determined linear trends for both variables using changes in the F_{\max} -SWI₅ relationship but keeping SWI₅ fixed to that experienced in the first three-year window of the observational record (1982–1984). As running means were used to construct the time series, non-independent running-mean blocks were removed before determining the strength and significance of trends.

CMIP5 simulations

We analysed output from ten CMIP5 coupled carbon-climate models (Supplementary Table 1) obtained from the Program for Climate Model Diagnosis and Intercomparison Earth System Grid (ESG) (<https://esgf-node.llnl.gov/search/cmip5>). The land components of these ESMs differ in their representations of vegetation types, soil properties, human disturbances, and carbon and nitrogen pools. We used model outputs of leaf area and air temperature at native spatial resolution, and converted to the fAPAR using the standard conversion of Beer's law, which accounts for the exponential decline in absorbed radiation with increasing leaf area. Values of F_{\max} , F_{95} and SWI₅ were calculated through a functional response analysis, as with the remote sensing observations. We used historical simulations (1980–1990) for the comparison of spatial responses of F_{\max} with SWI₅, and projections of future monthly temperatures from 2010–2100 under two RCPs: 4.5 and 8.5.

Code availability

All code relating to this study is available from the corresponding author upon request.

Data availability

The data that support the findings of this study are publicly available. The satellite fAPAR data are hosted on NASA NEX (see instructions at <http://sites.bu.edu/cliveg/datacodes/>). The CMIP5 simulation outputs are available from the Program for Climate Model Diagnosis and Intercomparison ESG (<https://esgf-node.llnl.gov/search/cmip5/>). The climate data used (CRU3.24) can be downloaded from <https://crudata.uea.ac.uk/cru/data/hrg/>.

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